18

The Web of Life: Development over 3.8 Billion Years of Trophic Relationships

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"Continuing sequences of assemblies are the veins of evolution," wrote Rubenstein (1989, p. 132), but the scale at which he developed this theme was orders of magnitude smaller than the scale on which I shall develop the same idea. I argue that whole organisms have assembled into symbiotic associations of increasing biotic complexity, providing macroevolutionary advances beyond those explicable by gradualism. A symbiosis may begin as a parasitism and evolve into a mutualistic association, becoming so obligate that the original units act almost as one organism. Communities of these units form the basis for major adaptive radiations on this planet.

There is no adequate gradualistic explanation for the wonders of biotic nature and the rapidity with which terrestrial life radiated to fill this earth. The questions go well beyond how the elephant got its trunk. How did large tree-like plants evolve so rapidly within perhaps 50 million years after the colonization of land by photosynthesizing organisms? How did large herbivores evolve? These are the questions I will address, albeit in a very crude manner.

The contribution this paper makes is not to symbiosis as a creative force, because this has been established (see, e.g., Margulis 1981). Rather, I emphasize that the origin of symbionts is likely to derive from parasite-host relationships and to evolve into mutualistic symbioses, providing the basis for extensive macroevolution and adaptive radiation. I will use the terms *mutualism* and *mutualistic symbiosis* interchangeably, although the latter is more accurate (Smith and Douglas 1987).

Mutualists From Parasites

The general argument for the acquisition of beneficial symbionts from parasites is as follows. When two species interact, there are many possible relationships: competition (−, −), to amensalism (○, −), predation and parasitism (+, −), commensalism (+, ○), and mutualism (+, +) (figure 1) . Among all these relationships, the general tendency will be for natural selection to reduce negative effects and favor positive effects (Price 1984). Thus, parasitism may evolve toward neutralism, commensalism, and even mutualistic symbiosis. This does not mean, however, that all organisms ultimately should rejoice in an "orgy of mutual benefaction" (May 1981, p. 95); mutualistic associations are commonly antagonistic to a third species (Addicott 1981).

How, then, do these mutualistic associations develop? How are mutualists acquired? In my opinion there are two important routes for the acquisition of mutualists from parasitic organisms: a parasite of a host may evolve directly into a mutualist with that host, or a parasite of a host may enable another species to exploit that host by associating mutualistically with the parasite.

Because they are finely evolved for living intimately with other organisms, parasites have a predisposition, or preadaptation, for becoming symbiotic mutualists (Price 1980). Therefore, I would argue the point—not pressed by Margulis (1981) and others—that the evolution of the eukaryotes, the acquisition of organelles, and the evolution of biotic complexity have depended on the initial invasion of parasitic organisms, an invasion which became mutualistic secondarily. Of course, commensals could also evolve into mutualists (figure 1), although commensalism appears to be much more sporadic in nature than parasitism and thus provides a poorer source of relationships from which to develop novel associations.

An excellent model for this process has been developed by K. W. Jeon and co-workers (Jeon and Lorch 1967; Jeon 1972; Jeon and Jeon 1976; Jeon and Ahn 1978; Jeon 1987). A strain of *Amoeba proteus* became infected by a strain of parasitic bacteria in 1966. These parasitic bacteria originally had many deleterious effects (Jeon 1972; Jeon, this volume), but in only 200 generations (18 months) the *Amoeba* population had become largely dependent upon the bacterium. The mutualistic association had become established, and in 10 years 100 percent of cells formed clones in the presence of the bacterium. In

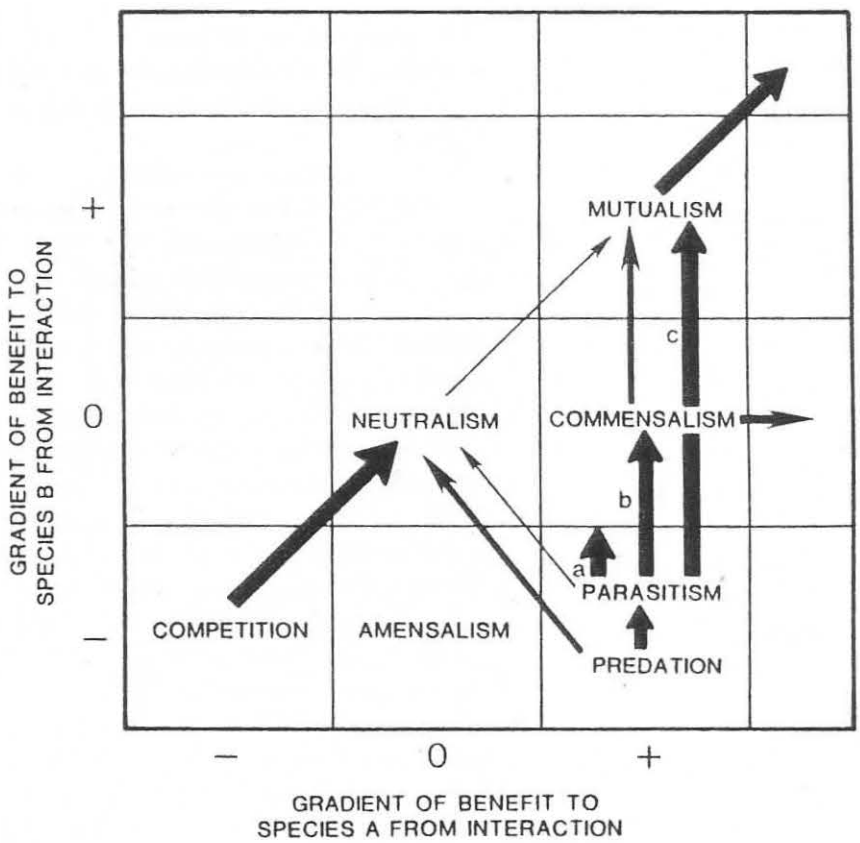

Figure 1
Predicted evolutionary pathways followed in two-species-interactive systems in response to natural selection for minimization of negative effects. Thick solid arrows indicate the most probable evolutionary routes, and thin arrows show other possible pathways. the possibilities for parasites to reduce impact on the host (a), to become commensals (b), and to become mutualists (c) are illustrated. From Price 1984.

evolutionary time, 10 years is almost instantaneous. This example illustrates the remarkably rapid shift from parasite to mutualist, a process which probably has been repeated millions of times in the evolution of life.

Atsatt (1988 and this volume) argued, as did Pirozynski and Malloch (1975), that land plants are "inside-out" lichens in which a semiaquatic green alga became the thallus and an aquatic fungus the endosymbiont essential in mineral nutrition for the new association. In Atsatt's words, "it began with fungal parasitism, may have evolved into a mutualism, and culminated in the acquisition of the fungal genome by the plant host" (1988, p. 17). What is more, the association between alga and fungus is proposed to be mediated by a virus-like element that makes possible a connection of cytoplasm between parasite and host across the cellulose cell wall. Atsatt's (1988, p. 21) argument for "a series of escalating parasitic events" in the evolution of land plants captures the essence of the theme I develop in more general terms here.

Another case of the shift from parasite to mutualist involves the development of mycorrhizal fungi, which are mutualists on the majority of terrestrial plants (Malloch et al. 1980).

Harley writes that "mycorrhizal fungi have evolved from aggressive parasites by progressive selection of nonlethal varieties so that the symbiotic stage becomes indefinitely prolonged" (1972, pp. 28–29). Some species of fungi are still mycorrhizal on some plant species and parasitic on others. Fungus and plant mutualisms also include endobiotic fungi which produce toxins effective against the plant's insect and mammalian herbivores; again these endobionts were derived from parasitic fungi (Carroll 1988; Clay 1988). Thus, the evolution of large plants is intimately associated with the utilization of parasitic species, ultimately as mutualists. And, of course, large animals frequently depend on large plants as a food source, or at least as a substrate to support the microcosms in their guts. The potential for parasites ultimately to benefit their hosts is obviously widespread.

The second important route to acquisition of a mutualist is for the parasite to mediate the interaction between its host and another antagonist of the host. This case is developed extensively in Price et al. 1986 and in Price et al. 1988.

One example is that of the blue-stain fungal pathogens in the genus *Ceratocystis*, which have long been parasites of coniferous trees. Many species of bark beetle in the genus *Dendroctonus* are mutualistic with

these fungi (Whitney 1982). The fungi are vectored by mites, which are phoretic on the beetles (Bridges and Moser, 1983), to live trees; they invade the tissues of their host and suppress its resistance by resinosis. As a result, the beetles breed successfully in the cambium of the tree, and their progeny transmit the fungus again. In fact, *Dendroctonus* is the preeminent genus of parasites among bark beetles because they attack healthy trees, whereas most species of bark beetles attack only dead or dying trees. By association with the fungal parasite, *Dendroctonus* has very successfully moved from saprophyte to parasite.

Another case concerns ichneumonid wasps whose larvae are endoparasitic on other insects, although the origin of the mediating parasite is less clear. The larvae can survive in the host only in the presence of a virus transmitted by the female wasp and injected with the egg (Vinson et al. 1979; Edson et al. 1981). The virus suppresses the immune response of the host, so the wasp egg survives and is not encapsulated and killed by host hemocytes. It is very likely that the acquisition of this viral mutualist occurred early in the development of endoparasitism in these wasps and was significant in the adaptive radiation of the group, resulting in tens of thousands of species.

Thus, when we look at the intervention by parasites in feeding by organisms on such refractory material as plants, with their cellulose cell walls, lignified xylem, and tough bark, it becomes evident that food webs based on plants are strongly affected (figure 2). In many cases, metazoans, which do not possess cellulases, utilize cellulose in plants by associating with bacteria, protoctists, or fungi, which are able to synthesize cellulases. Although the microorganisms were probably parasitic first on the plant or on the herbivore, major radiations have resulted from this mutualistic association: about 2000 species of termites, over 10,000 species of wood-boring beetles, and about 200 species of Artiodactyla (deer, antelope, camels, etc.). The last group contains many of the large herbivores conspicuous on the grasslands of Africa, which rely heavily on archaeobacterial methanogens for decomposition of plant food.

Nematodes parasitic on beetles can survive only when bacteria are present which produce antibiotics preventing the decay of host tissue. One example of this type is provide by *Neoaplectana* and the bacterium *Xenorhabdus* (Maggenti 1981; Paul et al. 1981, Nealson, this volume).

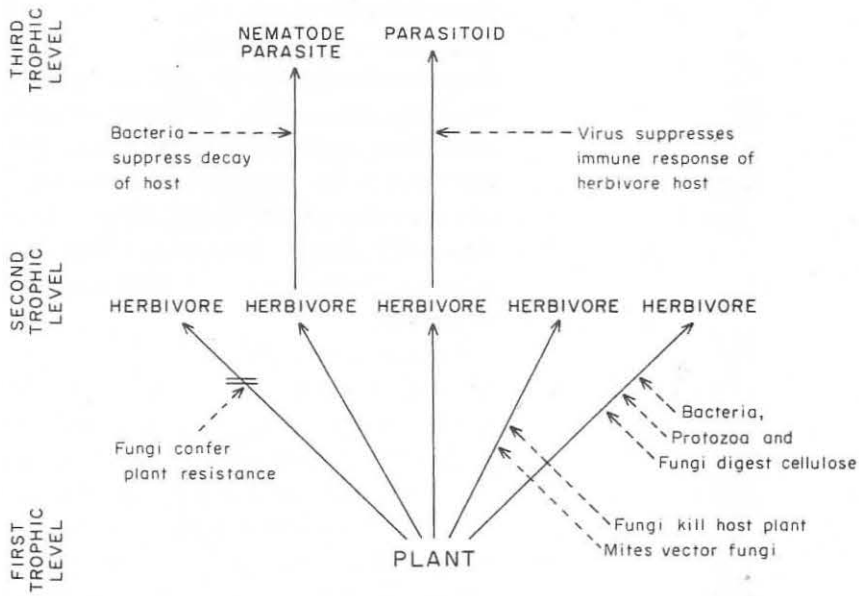

Figure 2
A summary of some important links between herbivores and plants, and parasites of herbivores and their hosts, that are facilitated by associated parasitic/mutualistic species. Specific cases given in the text illustrate the common microbial intervention between interacting macroscopic organisms.

I find the evidence overwhelming that parasites have provided important building blocks in the evolution of biotic complexes and still play vital roles in trophic relationships. The majority of feeding relationships between plants and herbivores and their parasites are probably mediated by symbionts, accounting for over half the species on Earth (table 1). Once herbivores and their associates accomplished the difficult task of converting plants into animal protoplasm, it was simple for large predators to evolve, probably without the need for symbionts to mediate the conversion of food.

Nesting in the Evolution of Life

Thus, when we gain a microscopic perspective of relationships between organisms, we obtain the strong impression that the evolution of the five kingdoms of organisms, as proposed by Whittaker (1969), has depended on a nesting of derived groups within the capabilities of the earlier groups (figure 3; see also Price 1988). Through many

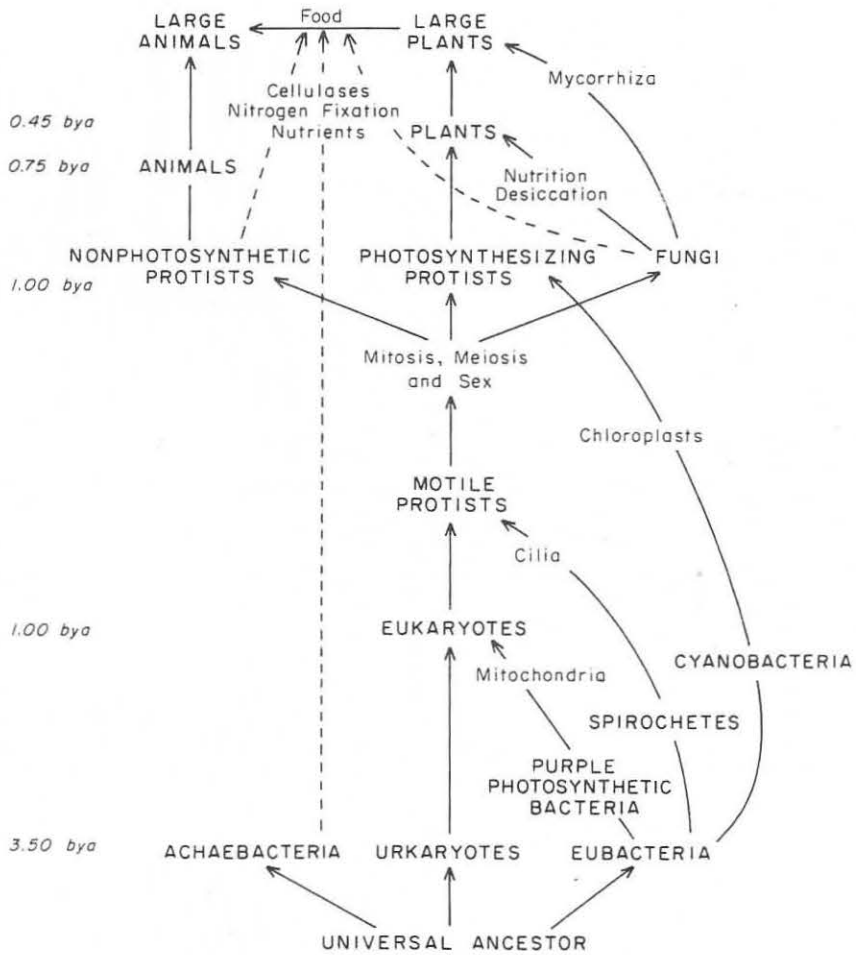

Figure 3
Major steps in the evolution of complex design of organisms and complex interactions resulting in webs of interacting organisms discussed in the text. Capitalized names are taxa of organisms or groups of taxa. Solid lines with arrows indicate links between evolutionary steps, and the contributions made by the taxa in the evolution of biotic complexity are given in capital and lower-case lettering. Dashed lines indicate the utilization of members of early kingdoms to enable the utilization of plants by large animals. For example, the methanogenic bacteia, important as mutualists in the ruminant gut, are members of the Archaeobacteria. This figure is simplified purely to illustrate some of the linkages in the evolution of biotic complexity, and is based on references cited in the text.

Table 1
Some examples of major adaptive radiations probably involving parasites evolving into mutualisms, with estimates on the extent of radiation. Note that the land plants, the invertebrate herbivores, and the parasitic wasps add up to 54 percent of the Earth's species.

	Extent of radiation*			
Radiating macroorganisms	Associated microorganisms	Number of species	Percent of species on earth	Source
Land plants	Aquatic algae and fungi	300,000	21	Pirozynski and Malloch 1975 Atsatt 1988
Land plants	Land plants and fungi as mycorrhiza	280,000	20	Malloch et al. 1980; Harley 1972
Invertebrate herbivores	Insects and microorganisms	360,000	26	Buchner 1965; Martin 1987; Price 1984; Whitcomb and Hackett 1989
Parasitic wasps	Endoparasitic wasps and viruses	100,000	7	Vinson et al. 1979; Edson et al. 1981
Vertebrate herbivores	Artiodactyla and bacteria	200	<<1	Hungate 1975

*These estimates are based on Southwood 1978, Price 1980, and Strong et al. 1984, with some modification, and must be regarded as first approximations.

instances of parasitism resulting in mutualism, the complexity of life has increased. The niche space occupied by derived groups depends heavily upon the broader capabilities of the older kingdoms, which allow broader niche occupation (table 1).

The present ecology of many species essentially recapitulates the phylogeny of life on earth (Price 1988). The capabilities of derived groups depend on associations with the earlier taxa. Close associations have frequently passed from parasitic to mutualistic because the parasites are adapted for living in close association with the host.

With a clear perspective of time, we see that microbial life has had billions of years (perhaps 3.8 billion years; see Woese 1984) to radiate into every conceivable quarter of the Earth, to solve every conceivable biochemical problem, and to surmount every obstacle of biotic interaction. By associating with these masters of intrigue and cunning, larger forms of life have thrived, and close association is the speciality of parasites.

What we see in a Noah's Ark perspective of biotic diversity—large plants and large animals—is actually large microcosms, many of them assembled through parasitic association. Parasites and their hosts have formed many of the building blocks for macroscopic life on Earth.

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